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OBSERVATIONS ON THE INFLORESCENCE  
OF APOCYNACEAE

(WITH SPECIAL REFERENCE TO THE AMERICAN GENERA  
OF ECHITOIDEAE)

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INTRODUCTION

As one reviews the advances of plant morphology during the past quarter century and more, one can scarcely avoid recognition of the fact that systematic botanists have made few recent contributions of note to our practical and theoretical knowledge of the structure of plants. This is in spite of the fact that the whole superstructure of plant classification rests upon an intimate knowledge of such considerations. The situation is incongruous with the superior opportunities which systematists enjoy for the advancement of the very basic and elemental science of plant morphology.

In the monographic method of investigation, the systematist has developed a tool of the very greatest potentiality for the exhaustive investigation of the morphology of plants. The accumulating multitudes of specimens in the great herbaria of the world which are available for study, particularly by the trained systematist, constitute an unsurpassed field for observations concerning the known flora in its entirety with the greatest ease. The important investigations of Solereder and

others upon the anatomy of flowering plants toward the close of the past century should remind us that herbarium specimens are capable of more uses in botanical research than ordinary dissection for the purpose of identification.

The possibility of studying the inflorescence of Apocynaceae largely by means of herbarium specimens was first appreciated by the present writer while studying in the Royal Botanic Gardens and herbarium at Kew during the summer months of 1930. The accurate picture of inflorescence structure which such specimens are capable of revealing was manifest at that time upon comparison of the exsiccatae with the abundant flowering material of *Allamanda Schottii* Pohl found in the conservatories containing *Victoria regia* and other tropical species. The gardens at Kew are perhaps the richest in cultivated species of Apocynaceae among the botanical gardens of the world, and the preliminary comparison of desiccated and living specimens of numerous genera of the family found there, made possible through the courtesy of the Director, Sir Arthur W. Hill, and others in authority, has proved of the utmost value in the subsequent studies of the inflorescence of which this paper is a condensed report. Since the commencement of the problem at Kew, the writer has continued the study of the apocynaceous inflorescence in the herbarium and living collections of the Missouri Botanical Garden at St. Louis.

The taxonomy of the Apocynaceae has claimed my attention for nearly a decade during which I have examined thousands of specimens of this family deposited in the principal herbaria and botanical gardens of America and Europe. The Apocynaceae are divisible into three subfamilies, the Apocynoideae, the Echitoideae, and the Plumeroideae. The scope of my taxonomic studies has included all the recognized genera and species of Apocynoideae and Echitoideae indigenous to the western hemisphere, as well as certain related genera of Europe and Asia (Woodson, 1930, 1933). Earlier studies have also included certain genera of Plumeroideae (Woodson, 1928a, b).

Structural advantages of the flowers of Apocynaceae which overcome the disadvantages suffered by desiccation to an appreciable extent in investigating the gross morphology of the

inflorescence can be indicated at this time. The flowers of the family as a whole are large, permitting even relatively small discrepancies of age to be visible in the development and size of the buds. The rule of large flowers is broken in such genera as *Forsteronia* and *Apocynum*, but even in such instances difference in stages of development of the floral buds is clearly indicative of correlated age and potential time of blooming, very important factors in the interpretation of modes of inflorescence. Relative age of floral members is also manifest in young fruit. A less obvious criterion in this connection is found in the accrescence of the pedicels. Since the pedicels increase in length and diameter for some time preceding abscission, even in the case of flowers which have failed of fertilization, a third important clue is present in herbarium, as well as in living, specimens to enable us to determine the phenology of the inflorescence with some precision.

The range of inflorescence structure exhibited throughout the family Apocynaceae comprises nearly all the more familiar types found among the flowering plants with the exception of such specialized examples as the capitulum and the ament. The most common inflorescence is the cyme, particularly the dichasium. At this juncture it becomes necessary to outline briefly the characteristic types of inflorescence amongst the Apocynaceae, both as a hasty survey and as a definitive introduction to the succeeding discussion. It will be found that the definitions of the inflorescence follow closely those of Jackson (1900).

*Dichasium*.—The dichasium is the most familiar type of cymose inflorescence throughout the flowering plants. It consists of a solitary flower terminating the primary axis of the stem or branch. Subtending this flower are normally two opposite leaves or bracts in the axils of which arise two secondary branches, each terminated by a flower similar to the first, but blooming subsequently and usually simultaneously. Such an axis system is called a simple dichasium. A continuous, or compound dichasium is frequently observed in the branching of the secondary axes in a manner similar to that of the primary, and so on. Such subsidiary components of a compound cyme are designated by the diminutive *cymule*. Dichasia are

frequently so composed of innumerable flowers arranged in impressive regularity. This type of inflorescence is found in numerous genera of Apocynaceae, including *Cycladenia* Benth., *Rhabdadenia* Muell.-Arg., and *Echites* P. Br.

*Aggregate Dichasium*.—A “panicle” is strictly defined as a compound inflorescence all axes of which are indeterminate. This interpretation was original with Roeper (1826), to whom we owe the first thorough-going discussion of the inflorescence. Nevertheless the general use of the term, persisting since the time of Linnaeus, still permits its use for virtually any compound inflorescence, preferably pyramidal and “loose” (Jackson, 1900; Gray, 1907).

The exact opposite of paniculate construction, one in which all axes of a compound inflorescence are determinate, has apparently never received a generally accepted name, although it, too, frequently is made to masquerade as a “panicle.” This type of compound inflorescence differs from the typical dichasium in that although the latter is the ultimate constituent of its construction, more than a single pair of branches occur, ordinarily at regular, decussate intervals below the determinate flower of the primary axis (cf. text-fig. 3, A). For want of a better name it is called an *aggregate dichasium*, since the inflorescence itself consists properly not of a single dichasium but of an aggregation, just as a raceme consists not of a single flower, but of an indefinite collection of them upon a specialized shoot. This type of inflorescence is conspicuous among Apocynaceae, as well as in certain other families, as Gentianaceae, being well organized in such familiar genera as *Apocynum* L., and *Forsteronia* G. F. W. Meyer,<sup>1</sup> accounts of which follow shortly.

*Cincinnus and Bostryx*.—In those cymes which consist of a single, sympodial axis, the monochasia of Eichler (1875), derivation from a dichasium has long been assumed by the substitution of a single flower for one of the equivalent inflorescence

<sup>1</sup> The limitations of publication preclude a complete category of the inflorescence structures of the genera of Apocynaceae which number at the present time more than two hundred.

branches. A bostryx is formed when the remaining subsidiary axis of such a modified dichasium is always either to right or to left of the determinate flower. This usually results in the somewhat curled inflorescence known as "helicoid," familiarly represented in many Boraginaceae. The maintenance of branching of such a highly modified dichasium alternately to right and to left, resulting in a somewhat zigzag sympodium widely known as "scorpioid" is characteristic of the cincinnus. In the bostryx and the cincinnus the sympodium is usually more or less curled or zigzag respectively. They may be simple throughout, or variously branched, by which they may recall their dichasial ancestry to a certain extent. Not infrequently the axis may become quite straight, however, when the nature of the sympodium must be distinguished by the usually paired pedicels in the axil of a single bract which is opposed to an "empty" bract upon the other side of the peduncle (cf. pl. 3, fig. 3). The peduncle is literally in the axil of the "empty" bract, which frequently becomes greatly dislocated in highly modified scorpioid and helicoid cymes, rendering their interpretation less easy.

The bostryx and the cincinnus occur widely throughout the Apocynaceae, the former in such genera as *Odontadenia* Benth., *Allamanda* L., and *Asketanthera* Woods., and the latter in *Prestonia* R. Br., *Temnadenia* Miers, and *Mesechites* Muell.-Arg. Scorpioid and helicoid modifications frequently creep into the ramifications of other cymose types, particularly when multiflorous.

*Raceme*.—Scarcely distinguishable from some highly modified examples of superficially indeterminate scorpioid and helicoid cymes is the truly indeterminate raceme. A typical raceme may be defined as a simple, pluriflorous, monopodial inflorescence in which a solitary pedicel is borne in the axil of a single bract. A pronounced peduncle is usually present which is of relatively greater length than the individual pedicels. Familiar modifications of the typical raceme are the spike, the corymb, and the umbel, based upon the relative length, or essential suppression of peduncle and pedicels. Typical racemes are infrequent in Apocynaceae, the principal genus bear-

ing them being *Mandevilla* Lindl., of some 108 species of the western hemisphere.

Jackson (1900) defines the umbel as "properly indeterminate," but recognizes the use of such a term as "cymose umbel" for those which are centrifugal and not centripetal in their floral development. Similarly, the same authority defines both a spike and a corymb as indeterminate. In these cases also it appears inevitable to recognize determinate as well as indeterminate spikes and corymbs. In such species as *Forsteronia paludosa* Woods., it will further be necessary to deal with a spiciform thyrses: a typical thyrses in which the pedicels are suppressed. Corymbs, in their typical, indeterminate sense, are restricted to racemose genera, as in *Mandevilla calacatensis* Mgf. The true umbel in Apocynaceae is unknown to this writer. Cymose, or determinate, corymbs and umbels are widely observed in such genera as *Prestonia* R.Br., *Thernardia* HBK., *Malouetia* A.DC., and *Asketanthera* Woods.

The spike, the umbel, the corymb, and other similar types, are doubtless merely modes of more fundamental types of inflorescence, and it would appear more simple in the end to use them in an adjectival manner, such as "corymbose raceme," and "corymbose cyme," than to limit the use of the word "corymb" to an indeterminate structure, in which case there would be an obvious necessity for another word to express similar, but determinate construction.

*Thyrses and Panicle.*—The thyrses and the panicle are recognizable as compound inflorescences in which the primary axis is indeterminate. In the true panicle, as represented by the common lilac, *Syringa vulgaris* L., the subsidiary axes, whatever their number, are likewise indeterminate. In the thyrses, however, the ultimate ramifications of the inflorescence are determinate, hence the "mixed inflorescence" of A. P. De Candolle (1827). The modification of the thyrses is excellently shown in the apocynaceous genus *Forsteronia*, amongst others, in which the determinate construction is variously expressed upon branches of differing magnitude throughout the entire inflorescence. The true panicle apparently is not found in any known Apocynaceae, although it is approached in certain species of

*Forsteronia*, a detailed account of which is reserved for succeeding paragraphs.

*Solitary Flowers*.—Solitary flowers are found in both terminal and lateral positions in the Apocynaceae. The former is typical of such genera as *Salpinctes* Woods., and such exceptional species of predominantly pluriflorous genera as *Echites crassipes* A. Rich. In all known instances, however, very inconspicuous, subtending bracts are usually capable of detection. In the familiar creeping myrtle, *Vinca minor* L., the solitary, lateral flowers are without the slightest evidence of subtending bracts. The different condition of the closely related periwinkle, *Lochnera rosea* (L.) Rchb., will be discussed presently.

Closely correlated with the predominance of cymose inflorescence in the family Apocynaceae is the occurrence with but few exceptions of decussate phyllotaxy. So much has been written concerning the spiral arrangement of appendages of the shoot as "primitive," a term of all too vague implications in many instances, that observations to the contrary might appear to have been suppressed by the sheer weight of consensus of opinion among morphologists. In the case of Apocynaceae, however, the reverse appears obvious.

Among the 132 genera recognized within the family by Schumann (1895) only twelve are characterized by spiral phyllotaxy. Of these, but one and two respectively are contained within the subfamilies Apocynoideae and Echitoideae, which have been found to have an elementary, or "primitive," carpological structure predominating (Woodson, 1930), while the alternate-leaved genera of Plumeroideae, characterized by the occurrence of generally more complicated, or "advanced," carpological conditions, number nine. Whorled phyllotaxy is found in fourteen genera of Plumeroideae and four of the Echitoideae enumerated by Schumann. In this connection it appears significant that of the eighteen genera with whorled phyllotaxy, no less than seven<sup>1</sup> are known to contain at least one species with normal, decussate foliage. In this, as in other

<sup>1</sup> *Aspidosperma*, *Condyllocarpon*, *Couma*, *Gynopogon*, *Laubertia*, *Macrosiphonia*, *Pycnobotrya*.

families, there is an obvious correlation of whorled and opposite phyllotaxy indicating the derivation of the former from the latter, possibly by the aggregation of nodes.

Such deductions as the immediately preceding receive additional support by observations on the young seedlings of *Amsonia* spp.<sup>1</sup> and *Rhæzia orientalis* (Dcne.) A. DC., the first stem-leaves of which are characteristically decussate. Two alternatives effect the adult, spiral phyllotaxy. In numerous instances among the seedlings under observation lateral buds were produced *in the axils of the cotyledons*. Upon subsequent development the arrangement of leaves upon such lateral branches was found in all cases to be normal for the adult condition of the species. The plumular shoot was short-lived. Somewhat less frequently among the seedlings a gradual change from decussate to spiral phyllotaxy was seen to occur upon the plumular shoot by the vertical translocation of nodes. The juvenile shoot was thereupon transformed directly to the adult condition. In innumerable instances more or less conspicuous vertical translocation of individual foliar nodes may be observed in species of Apocynaceae with normally opposite phyllotaxy.

Upon physiological-anatomical grounds opposite phyllotaxy and the occurrence of perfectly cymose inflorescence would appear to be unavoidably correlated. To many botanists the chief, if not the only, important characteristic of the cyme is the fact that for each axis a solitary, terminal flower exists which may be associated with a variable number of subsidiary floral members developing in basipetal succession. A most essential feature of the perfectly compounded cyme which has been overlooked generally, even by some students of inflorescence structure, is the almost geometrical precision which governs the expansion of its floral members. In such a simple dichasium of three flowers as has been described in a preceding paragraph, observable in innumerable genera of flowering plants in such families as Caryophyllaceae, Primulaceae, Gentianaceae, Apocynaceae, etc., the primary floral member termi-

<sup>1</sup> *A. Tabernaemontana* Walt., *A. brevifolia* A. Gray, *A. illustris* Woods., *A. pogonosepala* Woods.



nating the vegetative axis of stem or branch invariably blooms first. This is soon followed by the nearly simultaneous expansion of the two equivalent, lateral floral members immediately subtending.

If the dichasium be compounded to include for either branch a pair of lateral floral members subtending the secondary determinate pedicels, these will bloom shortly thereafter, in almost clock-like concert. This very impressive similarity of composition and unison of development of equivalent members of "perfect" cymes may appropriately be referred to collectively as its characteristic, or elemental "symmetry."<sup>1</sup> Common observation will probably lead one to object at this juncture that many, if not most, cymose inflorescences are not possessed of one or both of these "ideal" attributes under actual living conditions. Such is doubtless the case, and the remainder of this paper will be devoted to the occurrence of such irregularities among certain Apocynaceae and their possible evolutionary significance.

It is a fact quite easily observed that truly "perfect" cymes, whether di- or pleiochasia or derivatives of these, are found only upon flowering plants with opposite or whorled phyllotaxy. In no alternate-leaved species has this writer observed the strikingly symmetrical development of equivalent floral members so characteristic of the "perfect" (e. g. "ideal") cymes. The reason is doubtless anatomical and physiological: an inflorescence borne at the lower of two translocated nodes receives its vascular supply from the apical meristem somewhat earlier than the inflorescence immediately above. Hence subsequent development of the floral members is slightly in advance of that of the cyme immediately above, in spite of the fact that the two would be "equivalent" in the event of opposite phyllotaxy.

Although observations have been made over an unusually wide assortment of specimens during a number of years, as has been indicated in a preceding paragraph, the chief trends of

<sup>1</sup> This theory of the elementary symmetry of the ideal cyme will be found to place more emphasis upon the factor of time in development than the somewhat similar conception of "rhythm and symmetry" propounded by Goebel (1931).

the evolutionary development of the inflorescence in Apocynaceae may apparently be visualized from a review of a few characteristic representatives. In spite of the inevitable loss of minute detail, such an abbreviated account should possess a degree of clarity and simplicity difficult of attainment in a more extended, if more comprehensive account. It has been a matter of considerable disappointment that anatomical observations have been impossible because of the difficulty in securing fresh material of the critical genera. It is hoped that such data may eventually be secured to test the wholly gross morphological account which follows.

A final word of caution may be necessary to emphasize that perhaps no phase of the flowering plant's gross morphology is more variable than the inflorescence. The inflorescence is essentially a phase of branching of the shoot system, but it is vastly more complicated than vegetative branching, from which it has been derived. Hence the examples of inflorescence used to illustrate the observations which follow must be understood to represent *tendencies* perceived after wide study: they represent by no means the whole range of variation of a genus or species.

*Explanation of Symbols Used in Diagrams.*—In the diagrams illustrative of the succeeding paragraphs, dimensions have been maintained constant, despite disparities of the inflorescences in nature. The following symbols have been employed to denote floral members:

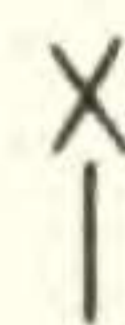
○ — floral bud.

□ — flower at anthesis or shortly thereafter.


▽ — fruit (in this and the preceding the relative size of symbols is indicative of the corresponding degree of development upon the actual specimen observed).


) — bract.

△ — leaf.

 — undeveloped bud, floral or vegetative.

/ — broken portion of specimen.

 — whole mature inflorescence.

 — immature inflorescence.

The limitations of diagrammatic representation render impractical an attempt to indicate the decussate or spiral composition of the inflorescence. Branches, pedicels, and bracts which appear opposite and in the same plane must be interpreted as naturally decussate: similarly with the alternate members appearing as in the same plane which must be construed as naturally spiral.

#### OBSERVATIONS

##### ECHITES P. Br.

Our present knowledge of the genus *Echites* (*sensu stricto*) is limited to seven species and a putative variety which may be separated provisionally into four sectional groups centering about *E. tuxtlenensis* Standl., *E. turbinata* Woods., *E. yucatanensis* Millsp., and *E. umbellata* Jacq., respectively. The aspect of the inflorescence of these species is reproduced in pls. 1-2. The best-known species of *Echites*, as well as the type of the genus, is *E. umbellata* Jacq., a liana occurring virtually throughout the Greater Antilles and extending to southern peninsular Florida, the Bahama Islands, and the coastal flats of northern Yucatan and British Honduras. The inflorescence of this species consists of one to several flowers, two, three, or four being the predominant numbers, borne in corymbose cymes. Tendencies of the inflorescence may be discussed briefly with the aid of five sketches provided in pl. 1.

The cymes of *E. umbellata* are predominantly alternate-lateral, but may be pseudoterminal as well. Such an individual is shown in pl. 1, fig. 5. In this case the axis is terminated by a

flower in full bloom. The two lateral branches bear one and two buds respectively, the solitary bud to the left being conspicuously larger than either of the two upon the opposite branch. The paired bracts of the branch to the right, in the axil of one of which the smaller lateral bud is found, indicate that the present condition was probably derived from a perfect cymule of three floral buds. Detection of a minute, abortive bud in the axil of such a superficially "empty" bract is usually possible upon careful dissection. At the base of solitary, lateral pedicels as that to the left of the figure are usually found a few rather indefinite, tiny bracts, also indicating that the uniflorous condition has probably been derived from a lateral cymule.

In fig. 2 of the same plate an inflorescence is shown in which the right lateral branch of the dichasium has failed to develop in the axil of its subtending bract which remains. The terminal flower is full blown. The left lateral branch consists of three well-developed, and one abortive, buds. The terminal bud of this cymule is about to expand, and is the largest of the three. The lateral bud to the left of the terminal is manifestly next in size, and is undoubtedly interpretable as the remnant of a reduced lateral cymule. The terminal bud of the right cymule is the smallest of the functional buds, and this fact appears to be correlated with the presence of the abortive, lateral bud at its base. Evidently the right cymule is slower to develop than the left because its axis has not been stripped of subsidiary axes dependent upon its vascular supply. At any rate, an examination of many specimens demonstrates an indubitable association of advanced development and potential blooming with increased reduction of the inflorescence.

Plate 1, fig. 1 illustrates a dichasium of three members, the terminal pedicel of which is bearing young fruit. The two lateral flowers are of approximately equal development. Two explanations of this cyme are possible: that the inflorescence as such is basic and elemental, or that the two lateral members have been reduced from pluriflorous, lateral cymules to the same degree, and thus expand with approximate simultaneity. Figure 4 represents a uniflorous condition of the inflorescence

of *E. umbellata*, not uncommonly found, in which, however, two abortive buds subtend. The truly uniflorous condition, without the presence of one or more abortive buds, has not yet been observed in this species.

In *E. crassipes* A. Rich., however, solitary flowers are borne, and with the aid of somewhat smaller foliage serve to distinguish this poorly understood endemic of Cuba. Even in the instance of this species, nevertheless, an indefinite and small number of minute bracts at the very base of the pedicel gives strong support to the assumption of reduction from a pluriflorous dichasium (pl. 1, fig. 3). The scope of variation in the relatively small inflorescence of *E. umbellata* increases with the number of specimens examined, and is plainly impossible to describe adequately at this time. An examination of even a few, however, is sufficient to form the opinion that the inflorescence of the species as a whole is undergoing reduction, and that the progressive reduction of a cymule tends to hasten the development of the remaining flower buds in relation to those of less reduced but equivalent cymules.

Plate 2 represents the inflorescence of four additional species of *Echites*. The group centering about *E. yucatanensis* is confined to Central America, and is most tangibly separated from the Antillean *E. umbellata* by the absence of the spiral contortion of the corolla-tube of the latter. Although the dichasium has advanced decidedly toward the umbellate condition, the general tendencies of the floral development of the former (pl. 2, fig. 3) are conspicuously similar to those of the latter species. In *E. turrigera*, known only from Guatemala, the inflorescence (pl. 2, fig. 4) is an almost typical, pluriflorous dichasium. Here also, however, the influence of unequal reduction of equivalent cymules in the disruption of the cymose symmetry is in unmistakable evidence.

Conspicuously smaller flowers set apart *E. tuxtlenensis* and *E. turbinata* from the other species of *Echites*. Here also the inflorescence is noticeably more extensive. In the former (pl. 2, fig. 1) a cyme is found in which the primary branching is dichasial and the subsequent composition helicoid. From the previous observations upon *E. umbellata* one may be led to

infer that here, and perhaps in all such helicoid cymes, the single, outer flowers of the sympodium, blooming only slightly subsequent to the expansion of the median, or terminal flower, have been hastened in their relative development by their previous reduction from a pluriflorous cymule.

The inflorescence of *E. turbinata* (pl. 2, fig. 2) is of puzzling nature, the first branching being typically dichasial, but the ultimate branching apparently partaking of the nature of the aggregate dichasium, since each of the three members is subtended by one or two small, probably abortive, floral buds, or by paired bracts. A logical explanation is that in this species a simple dichasium is being derived from the extensive modification of a more complex system. As this species, which is an endemic of Costa Rica, is extremely rare in herbaria, it may be hoped that a fuller understanding of its inflorescence will result from increased collections.

#### APOCYNUM L.

Promising clues to the origin of the aggregate dichasium are found in *Apocynum*, a genus of few species remarkably widespread over temperate North America. In *A. cannabinum* L., a ubiquitous weed of fields and roadsides, the inflorescence is predominantly terminal and multiflorous, consisting of a much ramified aggregate dichasium (text-fig. 1, A). Accompanying the terminal inflorescence are always two subsidiary, lateral shoots, both of which may bear a varying number of foliar nodes, in which case both eventually terminate with an inflorescence similar to the first. In many instances only one of such branches produces foliage; in this case the other produces directly an inflorescence similar to the first, but usually somewhat smaller. Naturally this second lateral inflorescence comes to full development much sooner than the first because of the elimination of the intervening foliar nodes. In many instances both lateral shoots may produce inflorescences directly without the production of foliage, in which case they become an integral part of the terminal inflorescence.

*Apocynum cannabinum* is an obnoxious weed largely because of its size and long period of bloom. These attributes are the

result of its ability to produce inflorescences through a relatively long season by means of its dichotomous or cymose branching. A much less pestiferous weed is *A. androsaemi-*

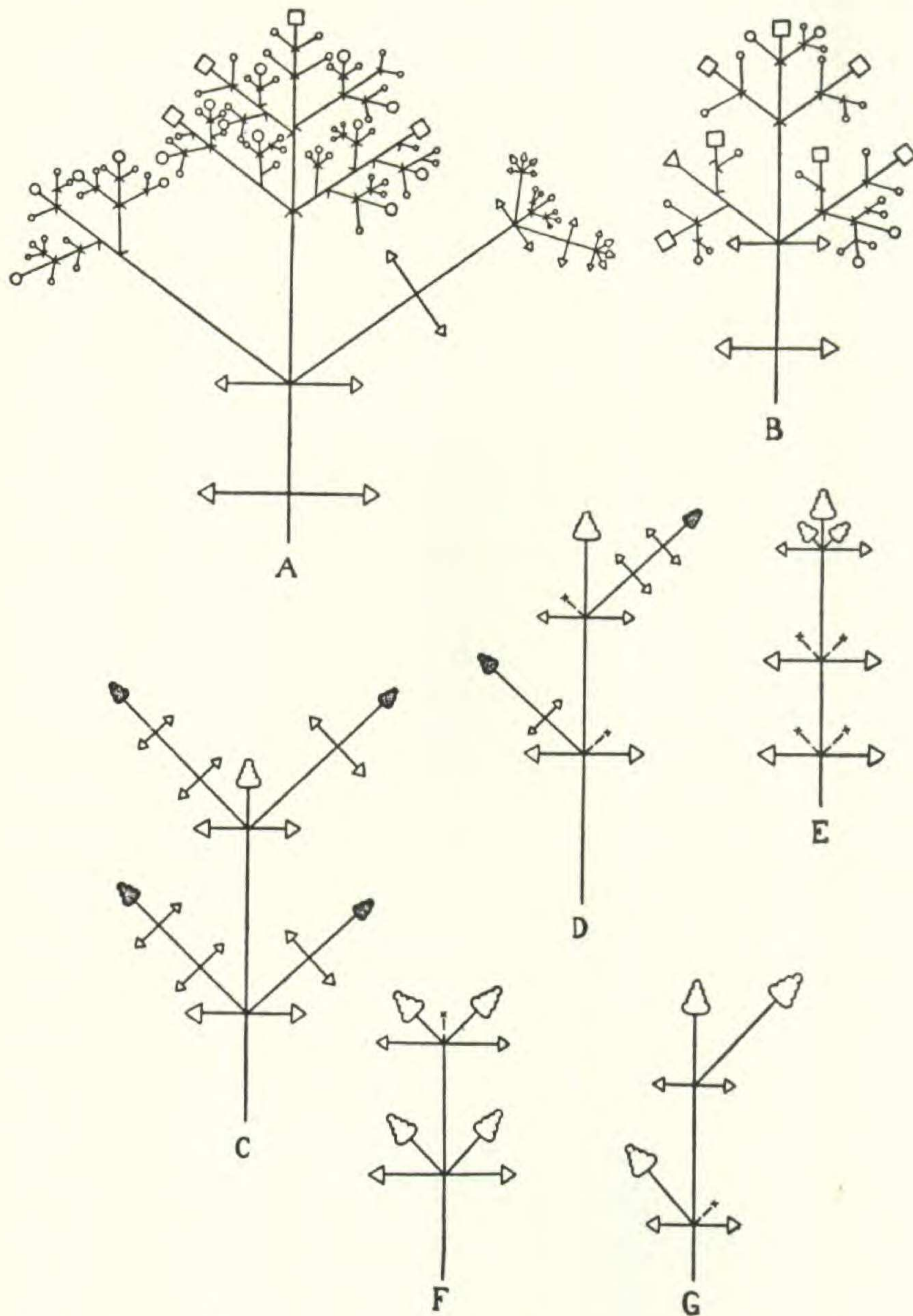


Fig. 1. Inflorescence structure: A—*Apocynum cannabinum* L.; B—*A. androsaemifolium* L.; C—*Forsteronia leptocarpa* (Hook. & Arn.) A.DC.; D—*F. paludosa* Woods.; E—*F. spicata* (Jacq.) G. F. W. Meyer; F—*F. amblybasis* Blake; G—*F. elachista* Blake. Explanation in the text.

*folium* (text-fig. 1, B), in which the lateral shoots accompanying the strictly terminal or median inflorescence do not tend to elongate as in the sister species. The blooming period, as well as the size of this species, is consequently relatively less.

“Aggregate dichasium” is evidently a well-chosen name for the inflorescence of *Apocynum*, from the phylogenetic standpoint; for if we read the data properly, it has been derived by the aggregation of a number of terminal dichasia through the elimination of the foliar nodes subtending them, hence the decussate composition of its branches. Recapitulatory evidence appears to occur in the inflorescence of *A. androsaemifolium* and other species, in which bracts of the median axis of the aggregate dichasium occasionally regain to a limited extent their foliar character.

*Apocynum* is apparently the only genus of Apocynaceae in which the origin of the aggregate dichasium may be read so easily. In the closely related genus *Trachomitum* Woods. of Eurasia, the inflorescence has become about as highly organized as in *Forsteronia*, an account of which follows. In *Poacynum* Baill., a close Asiatic relative of *Apocynum* and *Trachomitum*, the branches of the aggregate dichasium have undergone scorpioid modification.

#### ODONTADENIA Benth.

The evolution of the inflorescence of the echitoid genus *Odontadenia* would appear to approach the cincinnus from both the typical and the aggregate dichasium. Significant stages in this progression, drawn from representative species, are illustrated in text-fig. 2.

The inflorescence of *O. Hoffmannseggiana* (Steud.) Woods. is a variously modified, aggregate dichasium bearing few to relatively numerous flowers (text-fig. 2, A). In the specimen illustrated, which was collected by Tessmann in eastern Peru, two flowers are full-blown, one terminating the median axis, and one terminating the subsidiary axis to the right of the figure. It is clear that the floral bud terminating the equivalent, secondary axis to the left has failed to keep pace with the development of the sister determinate flower, and this fact is correlated with the fact that the cymule is composed of four flowering nodes and the one to the right of but two. It is significant also that the tertiary axes of the right cymule are in different stages of relative development: that to the left, consisting of



but one floral bud, is in a conspicuously more advanced stage than either of the three comprising that to the right. The same situation is found with respect to the two subsidiary cymules of

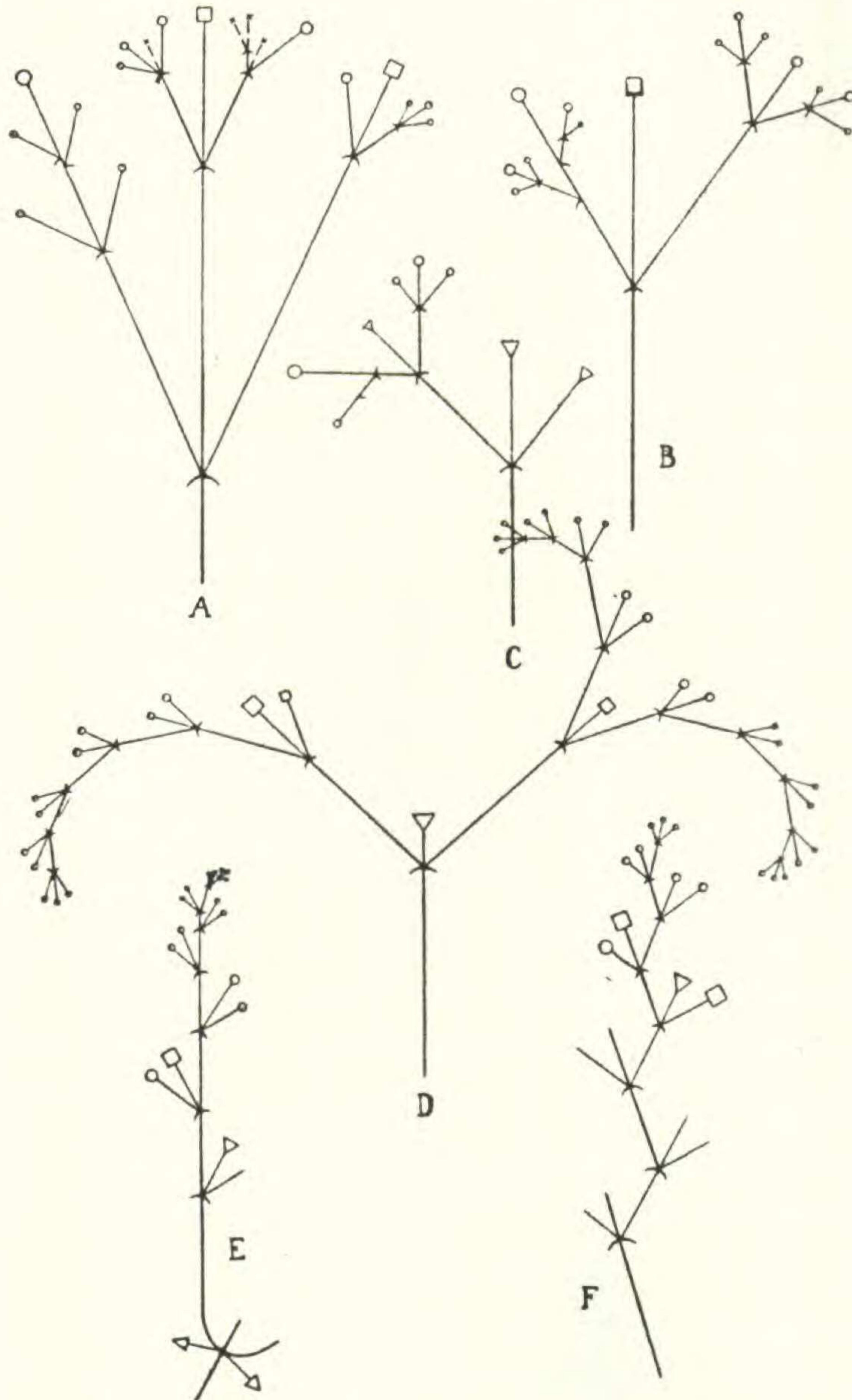


Fig. 2. Inflorescence structure: A-C—*Odontadenia Hoffmannseggiana* (Steud.) Woods.; D.—*O. laxiflora* (Rusby) Woods.; E—*O. polyneura* (Urb.) Woods.; F—*Angadenia Sagraei* (A.DC.) Miers. Explanation in the text.

the median axis, each consisting of four members, with abortion plainly in progress in the case of one and three of either cymule to the left and right respectively. The physiological result is clearly evident in the relatively advanced stage of development of the lone functional bud to the right.

The first stages of the development of a cincinnus are also observable in *O. Hoffmannseggiana*. In text-fig. 2, C, an instance is found in which the inflorescence consists of a primary, fruiting pedicel and two strongly unequal, secondary branches of one and six functional pedicels to right and left respectively. Although it happens that young fruit terminates both secondary axes of the dichasium, the size of the symbols is expressive of a significant disparity in relative development exactly like that found under similar circumstances in floral members.

An additional factor of great importance in the modification of the inflorescence is found in the effect of the vertical translocation of nodes. The translocation of the equivalent, tertiary cymules to the left of the inflorescence illustrated in text-fig. 2, B, shows that in such cases the members of the lower node are hastened appreciably in their development, even though those of the upper node may be somewhat more reduced in numbers. This fact, again, requires but an obvious anatomical-physiological explanation, since the lower node, differentiated first from the apical meristem, is effectively joined to the functioning conductive tissues of the shoot and root at a somewhat earlier time than the upper. Hastened development of its subtending members follows.

In *O. laxiflora* (Rusby) Woods. a peculiar modification of the inflorescence is found in which the main axis is regularly dichasial, but the secondary branch to the left has become helicoid by the repeated reduction of the right branch of each cymule to a solitary floral bud (text-fig. 2, D). The secondary branch to the right is compounded dichasially to the tertiary axes, which then become helicoid. The terminal flower of the secondary branch to the left naturally blooms before that of the branch to the right because of the greater degree of reduction of its axis.

The modification of the dichasium to a simple cincinnus is culminated in *O. polyneura* (Urb.) Woods. (text-fig. 2, E), in which a superficially indeterminate axis is compounded by paired pedicels borne in alternate succession subtended by one of a pair of bracts. The flowering axis is clearly a scorpioid sympodium, although it has lost the conspicuous zigzag aspect of less highly modified scorpioid inflorescences, as that of *Angadenia Sagraei* (A. DC.) Miers, illustrated in text-fig. 2, F.

## FORSTERONIA G. F. W. Meyer

The inflorescence of *Forsteronia* has been described rather loosely as a panicle. A thorough study of representative species discloses the fact that a true panicle is absent in all. Various modifications of the thyrses are predominant, varying from typical, pyramidal outline to structures which superficially resemble the corymb and the spike, through the elongation or the virtual elimination respectively of the subsidiary axes. The recent discovery of a species with the structure of an almost typical, corymbose raceme heightens the significance of the inflorescence structure of this genus, and renders its study of great value in the evolutionary history of flowering axes generally. Text-fig. 3 provides diagrams of the inflorescence of various representatives of this genus.

The inflorescence of *Forsteronia* is composed of many flowers of relatively small size, rendering analysis and interpretation somewhat difficult. Relatively young inflorescences, frequently collected separately and preserved in small packets upon herbarium sheets, have been found extremely useful for study, since they may be boiled *in toto*, restoring a semblance of the living posture. After study such specimens may be partially dried and pressed between blotters, from whence they may be returned to the herbarium packets after complete desiccation. Such procedure serves to emphasize the convenient use of herbarium specimens for the study of gross morphology beyond the usual practice of taxonomic identification.

The elemental type of inflorescence in *Forsteronia* would appear to be the many-flowered, aggregate dichasium, such as that of *F. corymbosa* (Jacq.) G. F. W. Meyer, *F. floribunda* (Sw.) G. F. W. Meyer, and *F. portoricensis* Woods. In such an inflorescence (text-fig. 3, A), the terminal flowers of the median, as well as those of all secondary axes, bloom with approximate unison. It is possible that this rather arresting phenomenon may be in large part due to the successive reduction of the number of floral members borne upon the secondary axes from bottom to top, resulting in the pyramidal outline.

Focusing our attention upon the individual composition of the lateral members, it is found that the tertiary branches are

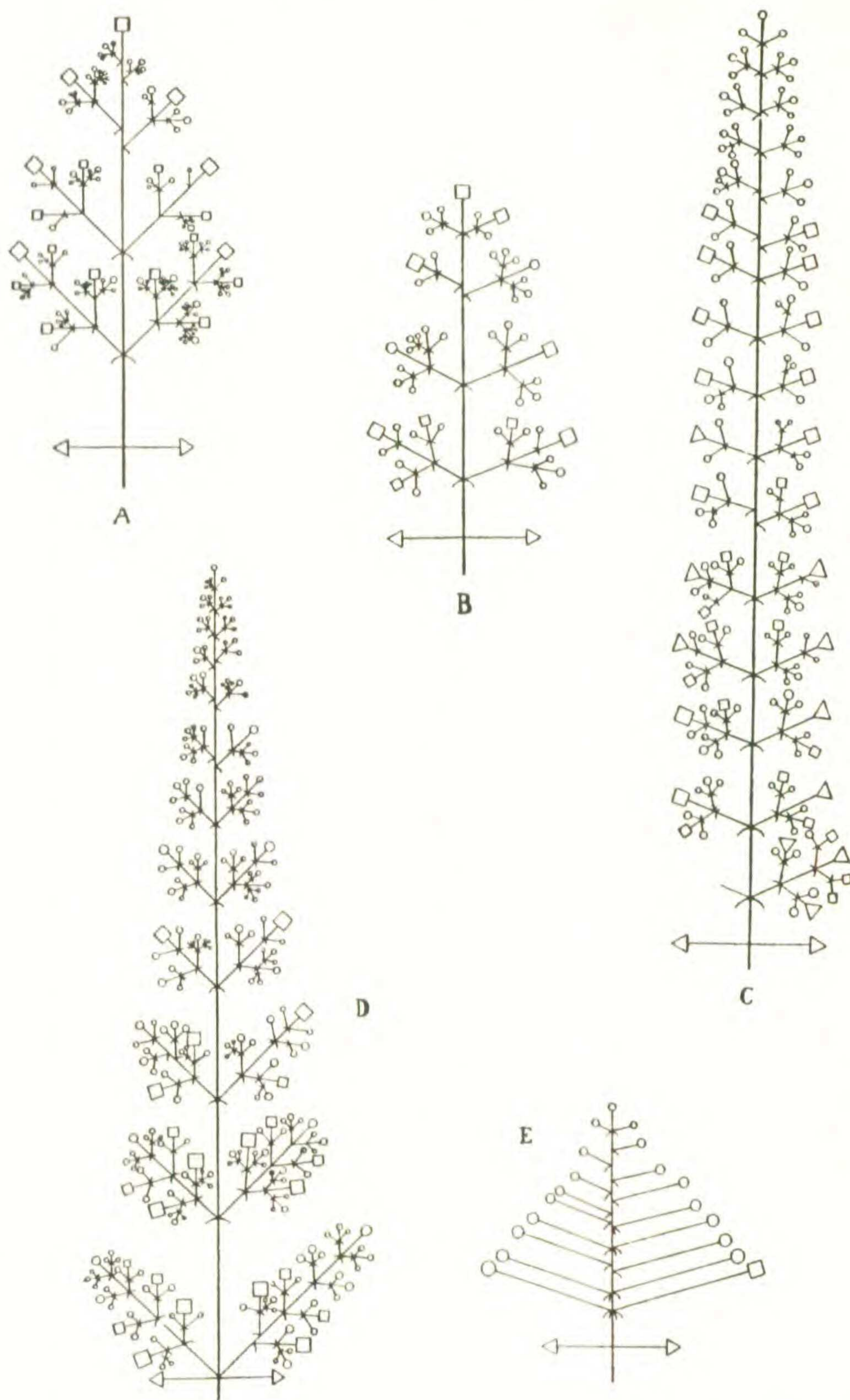


Fig. 3. Inflorescence structure: A—*Forsteronia corymbosa* (Jacq.) G. F. W. Meyer; B—*F. Velloziana* (A. DC.) Woods.; C—*F. thyrsoidea* (Vell.) Muell.-Arg.; D—*F. leptocarpa* (Hook. & Arn.) A. DC.; E—*F. simulans* Woods. Explanation in the text.

dichasial. The slight nodal translocation has apparently not succeeded in influencing effectively the phenology of the inflorescence.

The inflorescence of *F. Velloziana* (A. DC.) Woods. is a corymbose structure intermediate between the aggregate dichasium and the thyrses (text-fig. 3, B). In this inflorescence the symmetrical expansion of the terminal flowers of the secondary axes has been disrupted effectively by the reduction of certain branches, resulting in hastened development of certain of the floral members. The primary axis, however, is still determinate.

The first indications of the modification of the aggregate dichasium to the thyrses seen in *F. Velloziana* lead to the inflorescence type of *F. thyrsoidea* (Vell.) Muell.-Arg. (text-fig. 3, C), which is more or less typical of the thyrsoform structure, since the main axis is indeterminate with respect to the secondary axes, which still retain their dichasial composition variously modified. In this extensive inflorescence the small amount of variation in flower numbers among the secondary cymules from the first to the fifteenth pair of nodes can perhaps be explained by the assumption of reduction in number of floral members in basipetal succession. This assumption would also aid in explaining the acropetal development of the secondary cymules which is evident.

Typical panicles are apparently never found in Apocynaceae. The paniculate structure is closely approximated in the inflorescence of *F. leptocarpa* (Hook. & Arn.) A. DC., in which both the main and the secondary axes are indeterminate, although the tertiary and lesser branches remain determinate (text-fig. 3, D). The factors influencing the indeterminate modification of the primary axis of *F. thyrsoidea* may safely be supposed to have been identical with those effecting the indeterminacy of the secondary axes of *F. leptocarpa*.

Our knowledge of the evolution of the inflorescence in *Forsteronia* is culminated in *F. simulans* Woods., a rare liana of Colombia, in which the inflorescence is superficially a corymbose raceme with simple lateral pedicels. From the diagram of this "raceme" provided in text-fig. 3, E, however, have been



omitted numerous extremely inconspicuous bracts and abortive buds occurring rather irregularly upon the peduncle amongst the floriferous pedicels, which further exhibit a marked tendency of translocation. It appears obvious that this inflorescence has been derived from a thyrses characteristic of neighboring species.

One can scarcely fail to be impressed by the great range of modification of the inflorescence amongst species of *Forsteronia* which would appear to offer a most significant clue toward the solution of the questioned relationship of determinate and indeterminate inflorescences. The remaining known species of *Forsteronia*, numbering forty-one, present various gradients of the inflorescence structures of the five examples discussed in the preceding paragraphs. The great bulk of these show certain tendencies centering about the types represented by *F. Velloziana*, *F. thyrsoides*, and *F. leptocarpa*. It is significant that although the inflorescence has not been employed to a great extent in the taxonomic separation of the species in a recent revision by this writer, additional morphological criteria used in speciation have resulted in a concurrent classification.

Species of *Forsteronia* show a progressive transformation of vegetative to floriferous axes, distinctly recalling that previously discussed in *Apocynum*, but in greater variety. In *F. leptocarpa* (text-fig. 1, C), the terminal, aggregate dichasium is regularly accompanied by two lateral, vegetative shoots which continue the extension of the massive liana characterized by this species. Each of such vegetative branches may be compounded similarly. A somewhat similar method of branching is found in *F. paludosa* Woods., in which, however, a single lateral branch is developed in alternate axils of the decussate leaves. An abortive, or dormant bud is regularly found in the axil of the opposite node, which can become stimulated to growth upon injury of the stem above its occurrence (text-fig. 1, D).

In *F. elachista* Blake a lateral inflorescence occurs with the strictly terminal, occupying the alternate axils of the foliar nodes as in the vegetative branches of *F. paludosa* (text-fig.

1, G). In the case of numerous tropical Apocynaceae, notably species of *Odontadenia*, an indefinite number of cataphylls are found occurring at the base of such lateral inflorescences. These are not observed subtending vegetative branches, or they are inconspicuous. A natural assumption which presents itself is that the alternate lateral inflorescences of *F. elachista* are homologous with the vegetative branches of *F. paludosa*. In *F. spicata* (Jacq.) G. F.W. Meyer (text-fig. 1, E), terminal inflorescences are accompanied by opposite lateral inflorescences. In *F. amblybasis* Blake the tip of the branches frequently appears to produce a dichotomous inflorescence of equal halves (text-fig. 1, F). This phenomenon is shown to have been produced by the non-development of a terminal floriferous axis, traces of which can frequently be observed. Normal opposite-lateral inflorescences also occur in this species.

#### MANDEVILLA Lindl.

The large genus *Mandevilla*, consisting of approximately 108 known species, is typified among the American representation of the subfamily Echitoideae largely by simple, racemose inflorescence. The mode of raceme is diverse both in number of floral members and gross construction, varying from rather lax corymbs to elongate spikes amongst neighboring species. Diagrams of the chief types of inflorescence are provided in text-fig. 4.

It would appear highly significant that *Mandevilla* and *Forsteronia*, in which the tendency from determinate to indeterminate inflorescence is clearly evident, are closely neighboring genera. The foliar glands of the majority of *Forsteronias* are of almost the same structure and occurrence as those of *Mandevilla* subgen. *Eumandevilla*, and the construction of the anthers of either genus is closely similar. An additional factor of great importance is found in the stigmata, or "clavuncles," which are massive and umbraculiform in all species of *Mandevilla*, and in all save one species of *Forsteronia* are fusiform to subcapitate. The exceptional species of the latter genus is *F. simulans* Woods., with an umbraculiform stigma which could

scarcely be distinguished from that of a *Mandevilla*. It will be recalled that the inflorescence of *F. simulans* further approaches that of *Mandevilla* in its virtually racemose character.

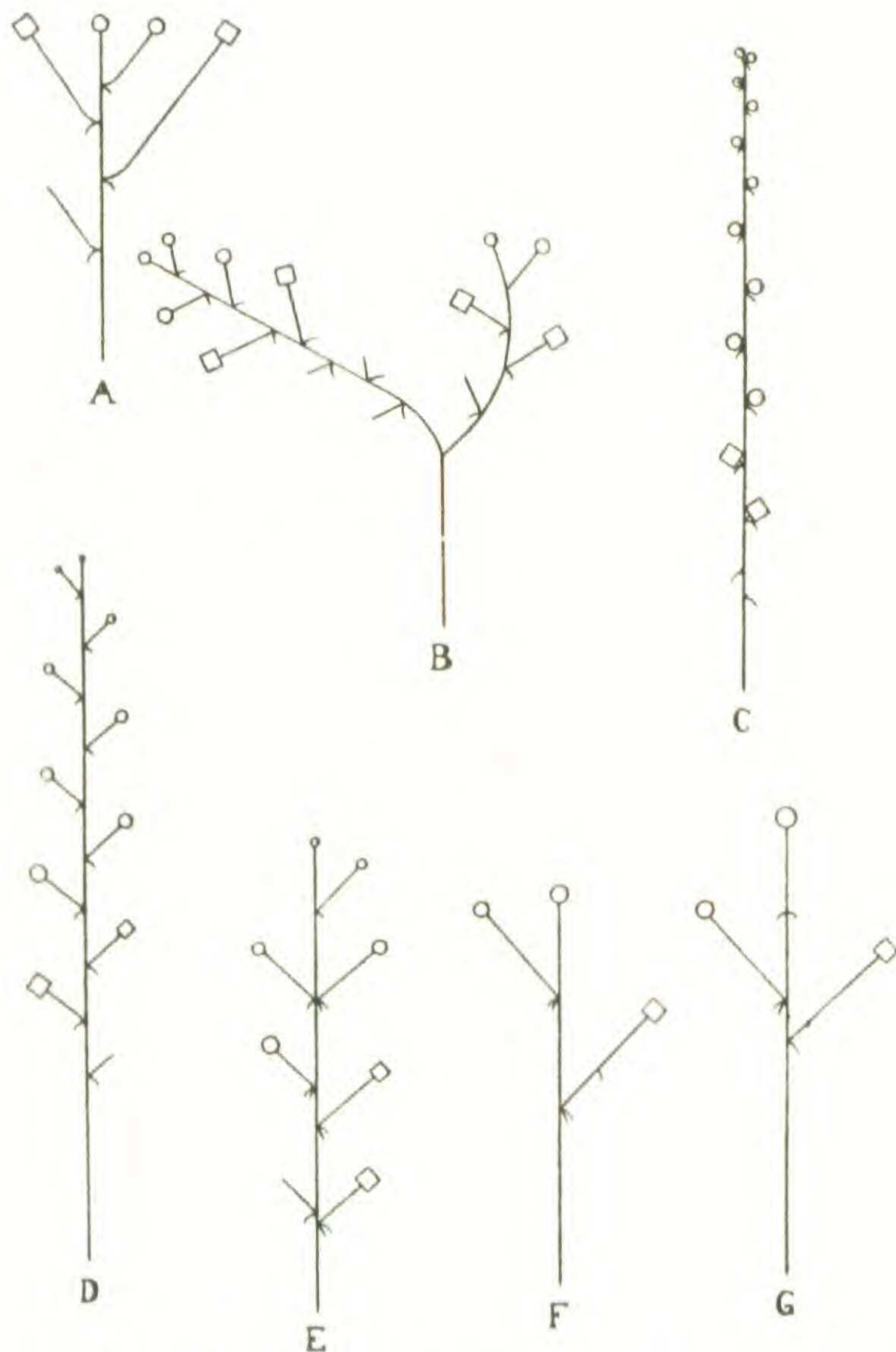


Fig. 4. Inflorescence structure: A—*Mandevilla calacatensis* Mgf.; B—*M. subpaniculata* Woods.; C—*M. scabra* (R. & S.) K.Sch.; D—G—*M. xanthostoma* (Stadelm.) Woods. Explanation in the text.

Although the inflorescence of the greatly preponderant number of *Mandevillas* may be characterized as simply racemose, a few, but highly significant exceptions occur. In *M. subpaniculata* Woods. (text-fig. 4, B), indubitable evidence of reduction from a compound inflorescence is found. That such composi-



tion is the effect of reduction, rather than of aggregation as was seen in *Apocynum*, for example, appears to be indicated in the fact that any such compounding is not in harmony with the vegetative symmetry of the shoot, but occurs somewhat irregularly, and often more obscurely than in the example figured. Less obvious clues leading to the conclusion of reduction are observable in the inflorescences of the closely related *M. Achrestogyne* Woods. and *M. bogotensis* (HBK.) Woods.

In *M. xanthostoma* (Stadelm.) Woods., an herbaceous and evidently a highly evolved member of this genus formerly included in the morphologically invalid genus *Dipladenia*, an interesting series of variations in inflorescence composition occurs which can scarcely be viewed other than as indicative of inflorescence phylogeny. A random collection of four such variations has been illustrated by diagrams in text-fig. 4, D-G, notes upon which follow:

1. Normal, or many-flowered, inflorescences of *M. xanthostoma* are of the typical, racemose type with alternate pedicels subtended by solitary bracts. Such inflorescences average roughly eleven to thirteen functional pedicels (text-fig. 4, D).

2. Abnormal, or relatively few-flowered, inflorescences tend toward a "pseudo-bostrychoid" racemose type with opposite pedicels, either or both subtended by more than one bract (text-fig. 4, E).

3. Multiplicity of bracts is frequently associated with opposite pedicels and reduced inflorescences, but not invariably (text-fig. 4, F).

4. The raceme may terminate indeterminately as well as pseudo-determinately by a terminal flower expanding slightly before the bud immediately below (text-fig. 4, G).

The unusual tendencies of inflorescence structure in such species as *M. subpaniculata* and *M. xanthostoma*, differing widely in their immediate intergeneric affinities, can easily be interpreted as indicating the evolution of the simple raceme characteristic of the genus as a whole from a primitive compound type similar to the thyrses. This evidence is entirely congruous with that found in the closely neighboring genus *Forsteronia*.

In this connection, the need of an anatomical investigation of those inflorescences, superficially racemose but with more than a single bract subtending each flowering pedicel, must be indicated. In the gentianaceous genus *Coutoubea*, it has been found that the inflorescence, described by systematists as a raceme, differs from a true raceme in the subtension of each flower by three to four inconspicuous decussate bracts. Recent investigation (Woodson, 1933) has disclosed the occurrence of occasional, abortive or dormant buds in the axils of these bracts which are detectable only in microscopic preparations. The "pedicels" of this inflorescence, therefore, are anatomically determinate axes, and the "raceme" itself could more accurately be described as a greatly reduced thyrsus.

Corymbose and spiciform modifications of the raceme in *Mandevilla* are illustrated by *M. callacatensis* Mgf. and *M. scabra* (R. & S.) K. Sch. respectively (text-fig. 4, A-C).

#### TEMNADENIA Miers

The dichotomous cincinnus is a type of inflorescence characteristic of a number of apocynaceous genera, in which the flowering axis consists of a more or less elongate, naked peduncle terminated by two bracts of various size and texture subtending roughly equal, scorpioid branches. Noting the absence of any interpretable structure in the crotch of the two frequently divaricate branches, one might be tempted to suppose the agency of dichotomy of the young growing initials of the inflorescence in early stages of development. Such superficially "dichotomous" inflorescences as those of *Temnadenia stellaris* (Lindl.) Miers (text-fig. 5, D) may occasionally be found to produce determinate flowers in the crotch of the scorpioid branches (text-fig. 5, E), however.

The suspicion that the inflorescence of *Temnadenia* has arisen from the elimination of the determinate flower of a continuous dichasium is heightened by an examination of the inflorescence of *T. stenantha* Woods. (text-fig. 5, F), recently discovered in northern Colombia, in which some of the uppermost branches may be clearly dichasial, with pedicels and bracts regularly disposed, although with unmistakable ten-

dencies toward the cincinnus. The lower branches of this inflorescence are of the superficially dichotomous development, even to the disappearance of the subtending bracts at the dichotomy.

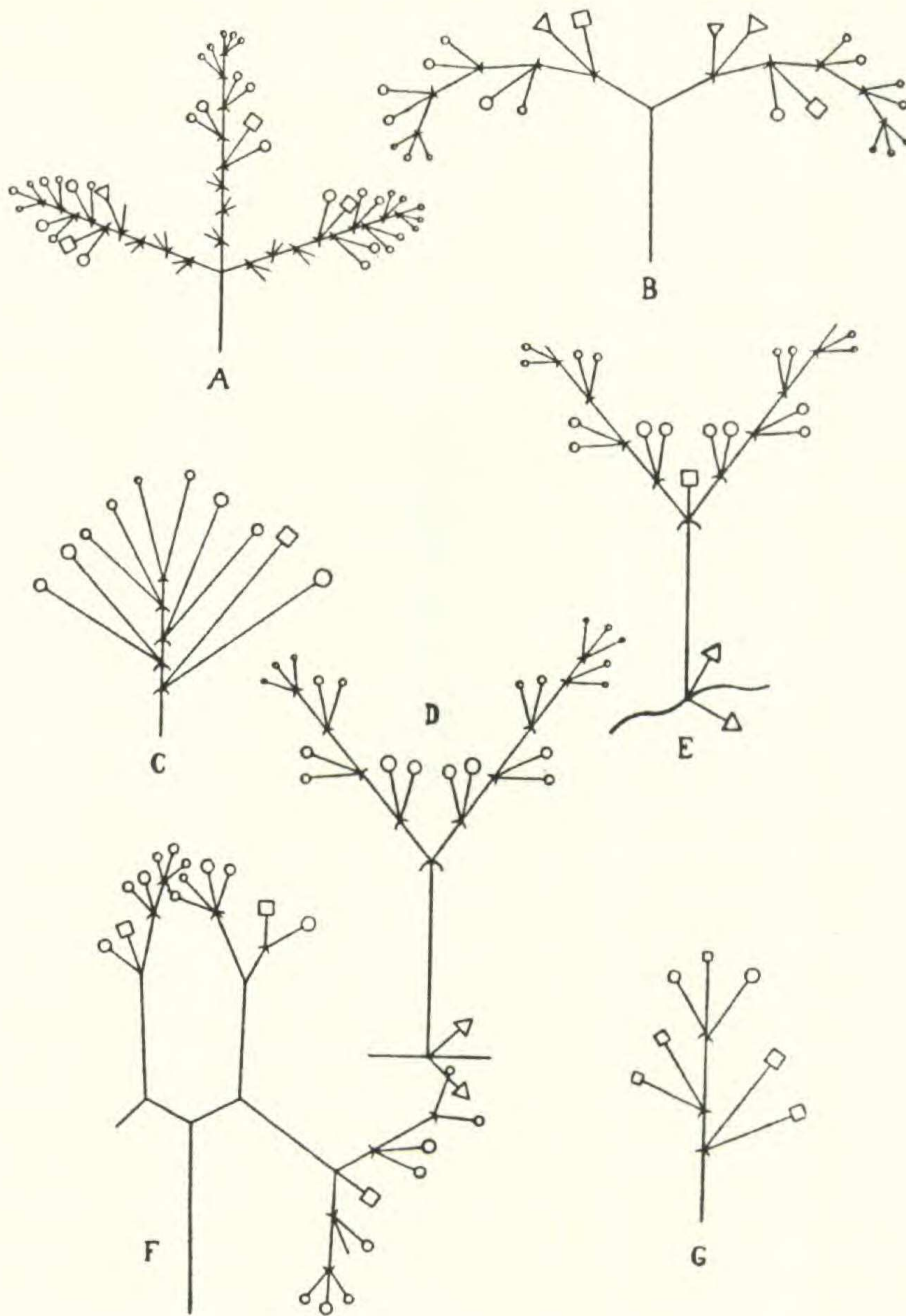


Fig. 5. Inflorescence structure: A—*Prestonia Meg'agros* (Vell.) Woods.; B—*P. portobellensis* (Beurl.) Woods.; C—*P. mexicana* A.DC.; D-E—*Temnadenia stellaris* (Lindl.) Miers; F—*T. stenantha* Woods.; G—*T. violacea* (Vell.) Miers. Explanation in the text.

The inflorescence of *T. violacea* (Vell.) Miers is usually simple and scorpioid (text-fig. 5, G), although individuals are not difficult to find in which derivation from such a floral axis

as that of *T. stellaris* is indicated by an inconspicuous subsidiary axis.

#### PRESTONIA R. Br.

The genus *Prestonia*, consisting of approximately fifty-four known species, is largely characterized by a type of inflorescence rather puzzling in its complications. In such inflorescences as those of *P. agglutinata* (Jacq.) Woods. (pl. 3, fig. 1) of the section *Coalitae*, and *P. quinquangularis* (Jacq.) Spreng. of the section *Acutifoliae*, the axis is simple and the pedicels scorpioidally arranged. These two species are selected for illustration since they exhibit to some extent the peculiar zigzag habit of the peduncle correlated with the scorpioid inflorescence of *Angadenia Sagraei*, evidently caused by the alternate left- and right-handed modification of a primitive dichasium, to which reference has been made previously.

Such species as *P. portobellensis* (Beurl.) Woods. (text-fig. 5, B) and *P. Meg'agros* (Vell.) Woods. (text-fig. 5, A) of the section *Annulares* exhibit a conspicuous di- or trichotomy of the inflorescence. In all such instances among species of *Prestonia* bracts are virtually lacking at the place of division of the floriferous from the naked branches, by which they lose the clue to a cymose origin found in species of *Temnadenia*. There appears to be little reason to doubt such dichotomous inflorescences as that of *P. portobellensis* to have been derived from the suppression of the determinate floral member and subtending bracts as in *Temnadenia*, indicating evolution from a continuous dichasium. If that interpretation be allowed, it would appear logical to assume the modification of the trichotomous inflorescences, represented by that of *P. Meg'agros* from an ancestral aggregate dichasium, such as that of *Forsteronia* species.

The section *Tomentosae* of *Prestonia* includes numerous species varying widely in their habit of inflorescence from simple to di- or trichotomous cincinni. In general, however, the tendency of inflorescence of these species is toward the condensation of the peduncle, producing such virtual umbels or corymbs as those of *P. mexicana* A. DC. (text-fig. 5, C, in which the pe-

duncle has been unnaturally extended to clarify its composition) and *P. brachypoda* Blake. The umbellate condition is closely approached amongst the species of *Thenardia* as well, in which the floriferous branches of a condensed, aggregate dichasium as that of *T. floribunda* HBK. (pl. 3, fig. 4) become successively foreshortened until the relatively elongate pedicels have the appearance of springing from a common receptacle subtended by numerous, involucre-like bracts as in *T. Galeotiana* Baill. The remarkable umbellate cymes of the genus *Malouetia* (cf. *M. Schomburgki* Muell.-Arg., pl. 3, fig. 2) have presumably had a similar origin.

#### MACROSIPHONIA Muell.-Arg.

Reduction from a pluriflorous condition has evidently resulted in the solitary, terminal flowers characteristic of the familiar North American species of *Macrosiphonia*. Since the evidence of reduction (i. e., position and composition of bracts and frequency of occasional lateral flowers) is used taxonomically in the delimitation of species, each will be discussed briefly.

*Macrosiphonia hypoleuca* (Benth.) Muell.-Arg., a low, suffrutescent species of the north-central Mexican plateau, is partially characterized by the terminal inflorescence consisting usually of a large, white, vespertine flower borne upon a relatively short pedicel subtended by two rather inconspicuous, paired bracts. Below the bracts is a peduncle ordinarily of about the length of the pedicel (text-fig. 6, A). The presence of the bracts reveals the compound nature of this superficially simple inflorescence, and their paired disposition would lead us to infer modification from a primitive cyme of which the present solitary flower might logically be viewed as the surviving determinate member.

Happily for this view specimens are not rare in which a second flower is found accompanying the determinate flower, obviously in the axil of one of the subtending bracts. An occurrence much less common is the formation of a complete three-flowered cymule (text-fig. 6, B). In at least one instance, however, a specimen from southern Mexico has been found in

which the appearance of a three-flowered raceme has been produced, presumably by the translocation of the normally opposite nodes.

*Macrosiphonia Macrosiphon* (Torr.) Heller differs from *M. hypoleuca* largely in the conspicuously foliaceous calyx-lobes, more or less petalaceous in the latter, and the broader, nearly concolorous leaves, which are conspicuously paler beneath in *M. hypoleuca*. The inflorescence of *M. Macrosiphon* also differs radically from that of its neighboring species, in the preponderant number of specimens examined, by the pedicel of the terminal flower becoming virtually sessile through the re-

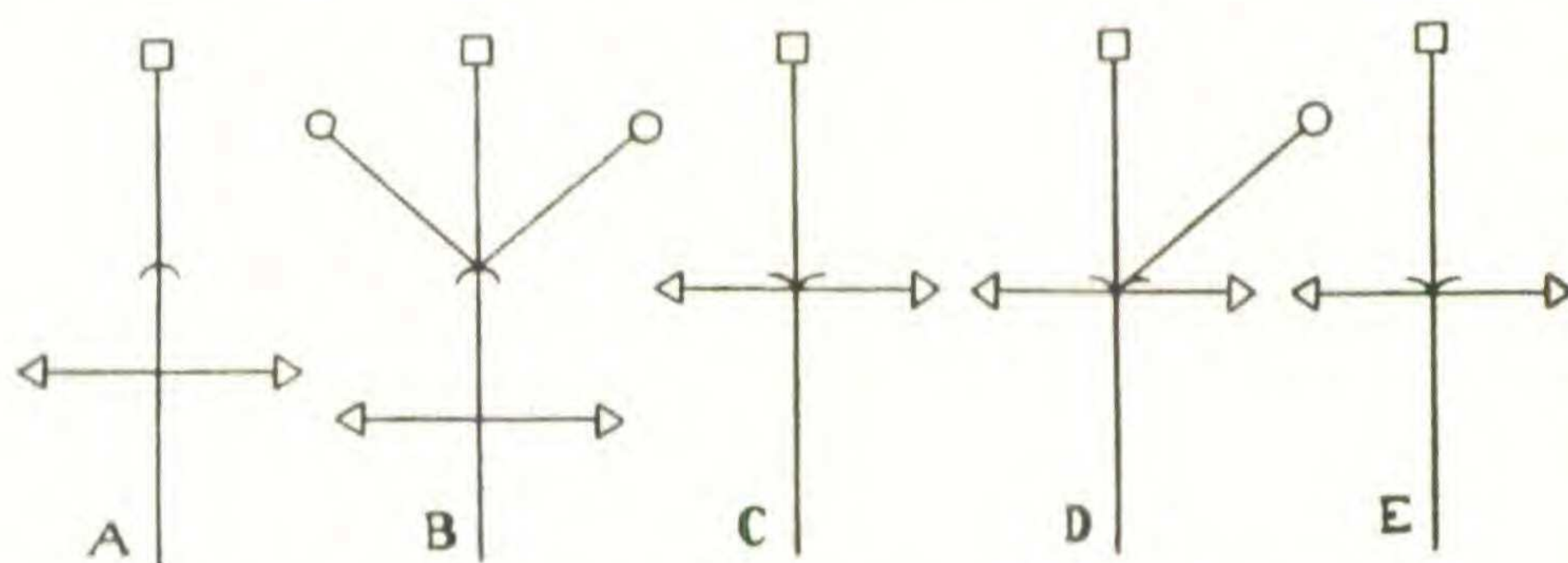


Fig. 6. Inflorescence structure: A-B—*Macrosiphonia hypoleuca* (Benth.) Muell.-Arg.; C—*M. Macrosiphon* (Torr.) Heller; D-E—*M. Brachysiphon* (Torr.) A. Gray. Explanation in the text.

duction of the peduncle (text-fig. 6, C). The primitively compound inflorescence is scarcely recalled save by the subtending, paired bracts which remain. These also may virtually disappear. No instances have been observed in which floral members have been formed in the axils of the bracts. The appearance of a perfectly simple, terminal flower in this species through reduction evidently depends upon the impending elimination of the already inconspicuous floral bracts. *Macrosiphonia Brachysiphon* (Torr.) A. Gray and *M. Hesperia* I. M. Johnston have been collected with both one and two flowers constituting the inflorescence (cf. *M. Brachysiphon*, text-fig. 6, D-E), which is practically devoid of a peduncle in either.

The opinion has been expressed elsewhere (Woodson, 1930) that the North and South American species of *Macrosiphonia* may have had independent derivation from some common stock such as that of the large and widespread genus *Mandevilla* or

its primitive progenitor. This conjecture receives support in the structure of the inflorescence of either group. That of South American species may be composed of either few or solitary flowers, which is somewhat less common. When few flowers occur, as in *M. longiflora* (Desf.) Muell.-Arg. (pl. 3, fig. 5), they appear in racemose disposition. Immediately subtending the calyx-lobes, however, is always observable a cluster of bracts which would indicate derivation from such a compound floral axis as that of the thyrses, for example. It has been pointed out previously that the mode of inflorescence in *Mandevilla* may be supposed to have been derived from a thyrses.

Additional instances in which a multiplicity of bracts supposedly remnant from a pluriflorous inflorescence is observable directly subtending a solitary flower borne in a lateral position are illustrated by *Elytropus chilensis* (A. DC.) Muell.-Arg. and *Macropharynx spectabilis* (Stadelm.) Woods. Specimens of either have been found in which one or two supernumerary floral members have been developed.

#### VINCA L. and LOCHNERA Rchb.

*Vinca minor* L. and *Lochnera rosea* (L.) Rchb. are among the most familiar garden plants. The former, popularly known as "running myrtle," is supposedly indigenous to the northern Mediterranean area, but has been so widely and so easily cultivated that it has become naturalized over a large part of western Europe and temperate North America. The latter, known as "periwinkle," has so successfully colonized the tropics of both hemispheres that considerable doubt surrounds the whereabouts of its original home, although it is probably from the Old World, the provenience of the two remaining species of the genus. A tender, ever-blooming annual, it forms an almost indispensable bedding plant in parks of the United States.

The inflorescence of *V. minor* (text-fig. 7, C) consists of solitary, lateral flowers. It is interesting to note, further, that the flowers appear only upon the semi-erect shoots produced in the early spring and summer from the creeping, perennial stolons. Not all the leaves of such shoots subtend flowers. The flowers

of *L. rosea* are produced regularly in lateral pairs subtended by the foliage leaves (text-fig. 7, A). The pedicels are arranged radially with respect to the stem axis and the subtending leaf; and the central flower always expands first. As the leaves are decussate, pairs of flowers are in nearly all cases found in the axil of only one of the paired leaves, ascending the axis spirally. It is clear that the axis of the inflorescence of *L. rosea* is a sympodium derived from a cincinnus.

Among many flowering individuals of *L. rosea* occasional abnormalities are found in which only a single flower is formed in the axil of a subtending leaf (text-fig. 7, B). Considering the very close relationship of the genera *Vinca* and *Lochnera*, it

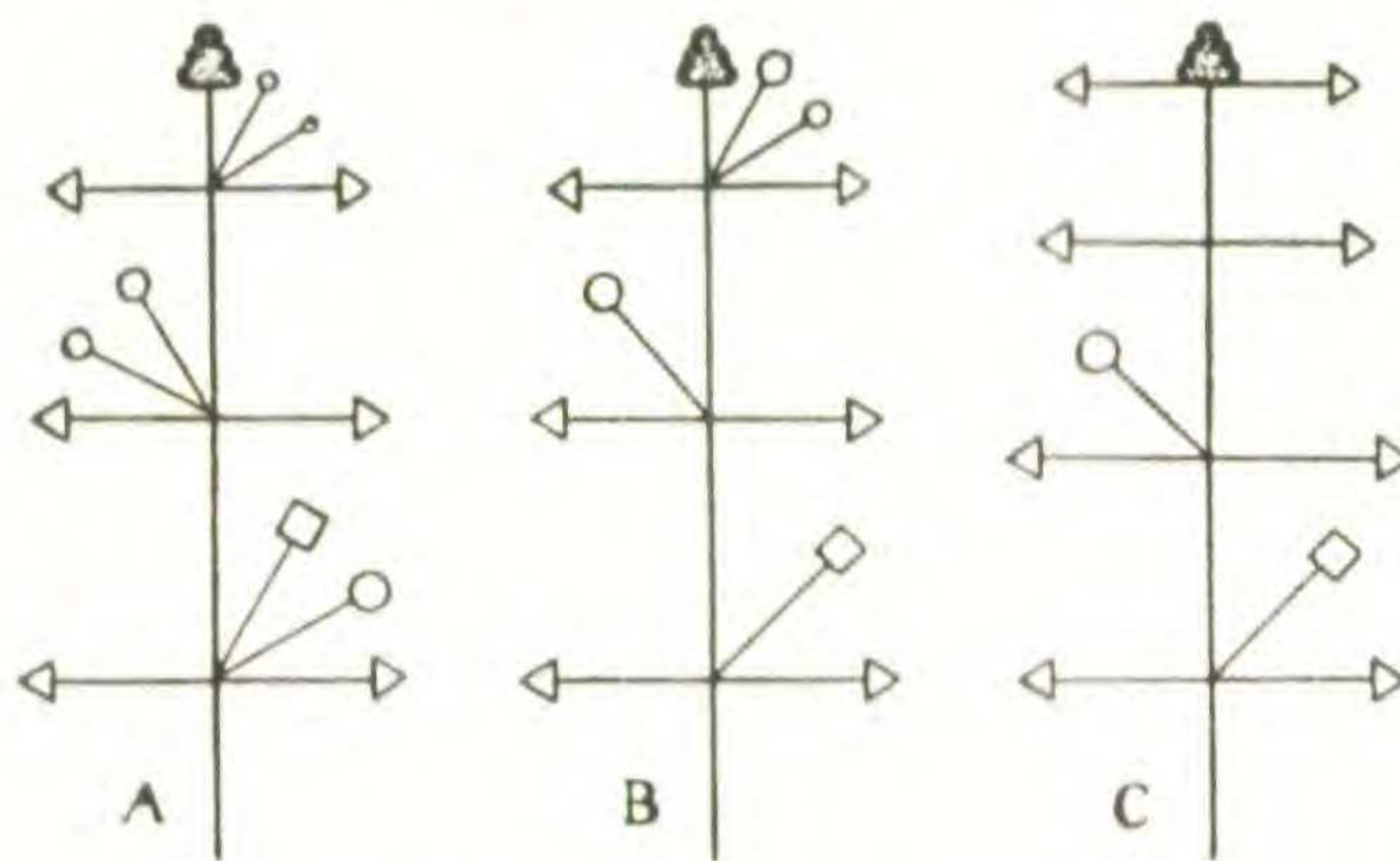


Fig. 7. Inflorescence structure: A-B—*Lochnera rosea* (L.) Rehb.; C—*Vinca minor* L.

seems more than likely that the indeterminate flowering axis of the former, bearing solitary, lateral flowers in spiral fashion, should represent derivation from such a sympodial axis as that of the latter.

#### DISCUSSION

The necessity of a general review of literature concerning the inflorescence is obviated by the very full historical account given by Parkin (1914), whose admirable treatment of the evolution of the inflorescence remains our most comprehensive. In view of the great importance of that memoir and of the somewhat different conclusions to which the present writer has arrived, it would doubtless be both appropriate and serviceable to combine a discussion of the apparent evolution of the inflorescence in Apocynaceae with a rather extended criticism



of the views so ably expressed by Parkin. In introduction, it is scarcely possible to recall too forcefully that this writer's opinions are based upon observations within a wide range of a single family. Although intensive study within a single natural group, even though large, entails indubitable benefits, it can scarcely be said to result in conclusions which are applicable to all groups equally. This will become apparent in a subsequent paragraph. On the other hand, it rarely happens that a general biological principle, such as that influencing the modification of the inflorescence, can be true of a single natural group, and of none of its closely neighboring relatives.

In his study of the inflorescence herbarium specimens were virtually ignored by Parkin upon the assumption of imperfect evidence offered by them. However, recourse was had to a large number of living plants selected from species commonly cultivated in English gardens. Special emphasis was placed in this selection upon dicotyledonous representatives of the so-called "primitive alliances," such as Magnoliales, Ranales, Papaverales, etc. Evidently inspired by the frequent occurrence of solitary, terminal flowers in plants belonging to such orders of established antiquity, Parkin was led to conclude that in the primitive inflorescence "flowers were originally borne in a solitary fashion, and that the clustering of them together without intervening foliage is a later development." Upon this assumption, he quoted the familiar Euclidean "reductio ad absurdum" to dispel Church's interpretation of the solitary flower of *Pyrus Cydonia* as a reduction from the many-flowered inflorescences of such species as *P. Aucuparia* (Church, 1908).

Parkin's statement that the solitary, terminal flower is an ancient structure approaches the platitudinous when one reflects that the flower itself may be defined as a highly specialized, contracted short shoot bearing a collection of sporophylls with or without an accompanying envelope. Quite likely, through past ages isolated progenitors of the modern Angiospermous flower, occurring terminally and isolated by intervening foliage, became aggregated to form a specialized branch system coincident with the evolution of the flower itself. But to trace the very foundations of the evolutionary development

of the inflorescence among the extant Angiospermae is a dangerous undertaking none the less. No doubt the floral organization of the Ranunculaceae may be considered as "primitive" from several points of view, but few would extend that interpretation to the herbaceous habit so conspicuously predominant in the family. Similarly, although *Papaver* is clearly a genus of great antiquity, we would be slow to describe its gynoeceum as "primitive" or elemental. It should clearly be recognized that groups of plants may possess palingenetic and cenogenetic characters side by side; our recognition of the former should not confuse our interpretation of the latter, although not to do so is manifestly difficult at times.

In supporting his contention of the primitive nature of the solitary, terminal flower among Angiosperms, Parkin cited the existence of terminal strobili in the Bennettitalean-Cycadalean plexus, now generally assumed to represent a primordium from which the flowering plants may have evolved. He noted, however, that the solitary, terminal strobili of the Cycads are occasionally accompanied by supernumerary members at the stem apex. The continuation of the vegetative growth is accomplished by a lateral bud, and a sympodium results. The anatomy of the axis of Cycads discloses the existence of a telescoped<sup>1</sup> sympodium essentially cymose in its composition, as Miss Smith (1907) has pointed out. In the Bennettitales, also, the branching of the Triassic *Williamsonia* (*Anomozamites*) *angustifolia* (Nathorst, 1902) and the Jurassic *Wielandiella* is of the sympodial type. The branching axis of the former, consisting of a system of relatively slender stems terminating in a strobilus surrounded by a rosette of leaves below which two equal branches are found similarly compounded, bears an unmistakable similarity to the modern dichasium of Angio-

<sup>1</sup> Apparently A. P. De Candolle (1827) was the first to use the metaphor of the telescope in describing extension and condensation of axes: "Je me ferais peut-être comprendre plus complètement par une métaphore bien grossière: supposons une branche florale organisée comme une lunette d'approche, qui porterait un pédicelle au haut de chacun des tubes qui la composent: que tous les tubes soient déboîtés et allongés, vous aurez une grappe; repoussez ces tubes à moitié, ce sera encore une grappe, mais très-courte; rentrez-les complètement, et vous aurez une ombelle terminale.

sperms, and the resemblance would appear to be more than fortuitous. It would appear a fruitless task to search for the earliest indications of the inflorescence among the extant flowering plants: the origin of the inflorescence is at least as remote as the origin of the flower, and a greater antiquity seems probable from the evidence of paleobotany.

Development of the pluriflorous inflorescence from the solitary, terminal flower is accomplished according to Parkin by the appearance of subordinate, lateral flowers literally "pushed out" of the axils of the subtending leaves of the original, terminal floral member. The continual "emitting" of subordinate flowers forms the first type of compound inflorescence: the dichasium. This process is illustrated in the genus *Papaver* by such species as *P. Rhoeas*, *P. strictum*, and *P. pilosum* in a series of floral accumulation, as we might express it for want of a better term.

The naivety of this conception of floral "emission" is heightened by the causal agent, ascribed by Parkin (1914) with some qualification to "a superabundance of reproductive material, more than the shoot could utilize in the formation of a single flower." This somewhat feeble effort to drag the continuity of the germ-plasm into the discussion of the inflorescence serves to illustrate rather indirectly the perplexing fact that although much is known concerning the "geometry" of plants, little indeed is understood of the causal mechanism responsible for it. Our easiest task, consequently, is to express structural modifications of plants in terms of the geometrical pattern approaching more nearly universal application throughout specific, natural groups. One might cite the example of dichasial branching, which is infinite in its theoretical extension. Practically, however, certain internal and external factors limit the expression of the dichasium to a definite numerical range of floral members in one species, and to a slightly different range in another.

In the end, the morphologist finds in nearly any highly developed group a "reduction series" in evolutionary history much easier to read than an "ascending series." Time and again the morphologist has found himself deceived by the ap-

parent "simplicity" of species and genera which have suffered reduction from the more elaborate geometrical pattern of their relatives during the inscrutable course of evolution. It should not be necessary to recall that our modern flowering plants represent a very ancient and specialized development whose foundations are still, and possibly always will be, exasperatingly obscure. The so-called "primitive alliances" are evidently scarcely more ancient, from available paleobotanical records, than others from which they have been separated by the imposition of an imperfect system of classification. The herbaceous habit of such genera as *Papaver*, for example, might be cited as but one evidence of a long and specialized evolutionary development.

From the evidence briefly reviewed for *Echites umbellata*, the evolution of the uniflorous condition from pluriflory through the agency of reduction appears plausible, for we have the evidence of reduction at hand in the form of "empty" bracts and occasional abortive buds. The opposite assumption, which would logically include the inference that such buds are in a nascent stage, would appear preposterous. This writer finds ample sympathy for the independent and earlier views of Church (1908) respecting the evolution of the inflorescence in *Pyrus* to which reference has been made in a preceding paragraph.

The result of reduction upon the development of the remaining floral members of the inflorescence described in the previous paragraph is strikingly similar to that of the old horticultural practice of "picking out the suckers," or "disbudding," in the cultivation of tomatoes, grapes, and other cultivated plants, by which the growers seek to influence the subsequent development of the remaining members. "Disbudding" is also practiced in the forcing of cultivated chrysanthemums, etc., and the time of blooming can be controlled largely through this agency. Gardeners using the same method in the cultivation of such plants as *Paeonia* have observed that plants which "disbud themselves," e. g., by natural abortion of floral buds, bloom earlier and have larger flowers than those whose full floral complement develops unchecked.

Much the same effect can be produced experimentally by amputating floral buds of such an inflorescence as the multiflorous thyrses of the apocynaceous *Amsonia Tabernaemontana* Walt. Precaution must be taken, however, to arrest the development of the buds at a sufficiently early stage and with the slightest possible injury. All experiments made in this manner have not been wholly satisfactory, due probably at least in part to the latter factor. Since it is impossible wholly to exclude the factor of injury, even slight success in modifying the symmetry of the cyme may be regarded as significant, the more subtle influence of natural abortion being beyond perfect imitation.

Concerning the transition of the indeterminate from the determinate inflorescence, Parkin (1914) envisions a process in which "the number of lateral floral shoots increase, so that the main terminal flower no longer blooms first. The flowers then tend to open in acropetal succession from the commencement. The next step comes about through the flower-buds of the uppermost part of the inflorescence never expanding; this part, in fact, becomes arrested in its development and finally aborts, leaving a mere filament or protuberance in its place. In this way the original terminal flower disappears. The inflorescence is now racemose." In the light of what the author has said as previously reported concerning the supposed primitive, few-flowered inflorescence, one can scarcely avoid confusion in attempting to harmonize this last statement with the innumerable-flowered cymes of *Statice* and the relatively few-flowered racemes of *Plumbago* among Plumbaginaceae, to cite only one example. From Parkin's statement one would be justified in expecting racemes to contain more numerous flowers than cymes. Such is scarcely the case. The flexibility of the extent of the cyme might be likened in potentiality to that of the compound interest table.

On the other hand, failure of the apex of the peduncle to produce a terminal flower is not an inalienable characteristic of the raceme. In racemes of but few flowers a terminal member frequently occurs. This has already been demonstrated for the genus *Mandevilla* of the Apocynaceae (cf. text-fig. 4, A-G).

In perhaps no other particular are the observations of Parkin and those of this writer in greater contrast than in the immediate agency involved in the transformation of the indeterminate from the determinate mode of inflorescence. Both views are based upon anatomical-physiological assumptions. The view of Parkin may be epitomized in the statement that as the lower floral members increase in number, the development of the apical members is hindered by the increasing demands upon the conductive facilities of the axis, supposedly. In the preceding observations among the Apocynaceae, on the other hand, a totally different process is adduced. It has been found in *Echites* that in the instance of two equivalent cymules of identical composition the *reduction* of one or more floral members of one will hasten the development of the other component members, thus effectively disrupting the characteristic "symmetry" of the two equivalent cymules. It has been inferred with ample evidence that the cincinnus and the bostryx have evolved from the dichasium in this family through the reduction of a whole cymule to a solitary flower, thus invariably hastening its development second only to the primary determinate flower with which it becomes associated.

It is understood that reduction has effected *one* of the lateral cymules of a continuous dichasium to the production of the cincinnus or the bostryx. The effect of the reduction of *both* lateral cymules of an aggregate dichasium may be computed artificially: its demonstration in nature is afforded in the large genus *Forsteronia*, by which it has been shown that closely related species intergrade from aggregate dichasial inflorescences to a raceme through various modifications of the thyrses.

Having traced the development of the more important types of determinate and indeterminate inflorescences amongst the Apocynaceae, it becomes easy to extend our understanding; by the reduction of the pedicel to derive the spike from the raceme, and by the reduction of the peduncle and the compensating elongation of the pedicel to produce the corymb and the umbel, which may evidently be derived from both determinate and indeterminate forebears. Although generalizations are fre-

quently weak in the face of detailed attack, it may be permitted to visualize the writer's conception of the evolution of the fundamental types of inflorescence in Apocynaceae as represented in text-fig. 8.

At this juncture prominence should be given to the fact that reduction of floral members does not always hasten the de-

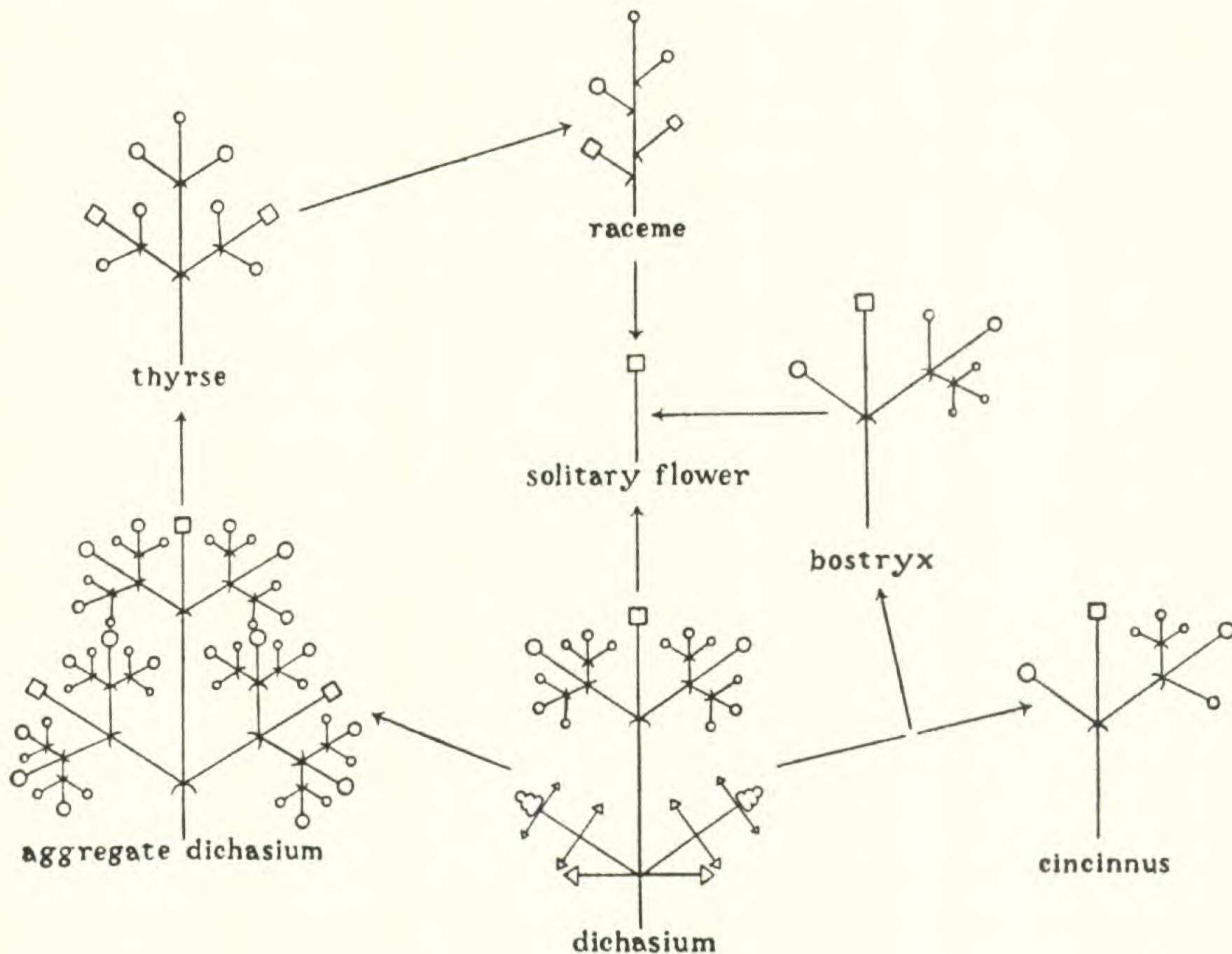


Fig. 8. Schematic diagram of the supposed relationship of certain types of inflorescence in Apocynaceae. Explanation in the text.

velopment of the remaining members of a cyme. Early in the course of these investigations recourse was had to members of other families to ascertain whether the same procedure is common. Selecting families containing familiar representatives bearing cymose inflorescences, it was soon found that the same principles discovered in Apocynaceae are apparently applicable in members of such families as Ranunculaceae, Rosaceae, Primulaceae, Gentianaceae, etc. In the family Caryophyllaceae, characterized by the predominance of the cyme, how-

ever, the principle of reduction in the disruption of cymose symmetry appears to be completely reversed. One needs but examine a colony of such a species as *Arenaria patula* to discover that the terminal flower of a somewhat reduced cymule actually blooms somewhat later than the terminal member of an equivalent, less-reduced branch. The reversal, moreover, appears widespread if not universal throughout the family, as well as in members of Convolvulaceae, and it would be odd indeed if it were unique among the flowering plants in this respect.

The solution of the enigma which is thus introduced, as well as the actual mechanism of the phenomena noted in Apocynaceae, etc., would appear to lie in a study of the anatomy of the inflorescence, a virtually untouched field since the rather few students of the inflorescence as a whole have limited themselves to gross morphology save in special instances. A decidedly hypothetical conception which must be tested by a future anatomical study of the inflorescence to explain the divergent results of reduction in Apocynaceae on the one hand and Caryophyllaceae on the other, might involve the divergent reduction of vascular tissues within the respective inflorescences: the reduction of vascular tissues and its attendant physiological effects possibly being limited to the pedicels of discarded members in Apocynaceae, thus redistributing the full flow of the conductive elements to the fewer floral members which would benefit accordingly; the reduction of vascular tissues in the Caryophyllaceae on the other hand taking place in the peduncular axes, thus hindering the development of the branch system as a whole. At any event, the primitive nature of the cyme in Caryophyllaceae should be established by future studies of the inflorescence of the group; here also, as in Apocynaceae, etc., the solitary flower is evidently a condition derived from pluriflory.

Minor points of criticism of Parkin's observations, in the light of the present writer's investigations on the inflorescence of Apocynaceae, may be dismissed without discussion. It should be noted that both are in agreement concerning the primitive nature of determinate and the derived condition of



indeterminate inflorescences. It is suspected that Parkin's inferences concerning the method by which the indeterminate mode was derived from the determinate were unfortunately affected by the fact that his illustrations include no perfectly symmetrical representatives of the latter. It is easily appreciated that the most characteristic features of the dichasium, for example, are lost in species with alternate, or spiral phyllotaxy, as has been indicated in an earlier section of this paper.

#### SUMMARY

The following conclusions have resulted from a study of the inflorescence structure of numerous representatives of Apocynaceae throughout the distribution of the family, as revealed by both living and herbarium specimens. Special emphasis has been placed upon the American representatives of the subfamily Echitoideae, an evidently natural group lately studied by this writer (Woodson, 1933) from the combined aspects of floral anatomy and taxonomy.

1. The dichasial cyme appears to be the primitive inflorescence of the family.

2. The symmetry characteristic of the composition and sequence of development of equivalent cymules of the inflorescence of *Echites umbellata* Jacq. is found to be profoundly modified by unequal reduction of the component floral members. Reduction of one or more lateral members of a cyme is found to accompany a somewhat hastened development of the remaining members. This effect of reduction appears constant, or relatively so, amongst Apocynaceae and certain other families, but appears to be reversed in Caryophyllaceae (and Convolvulaceae) for reasons which are briefly conjectured. Such an agency is found to parallel long-established horticultural practices, such as "picking out the suckers," and "disbudding."

3. Reduction of a single branch of a continuous dichasium always to the right or left of the determinate flower, or to the right and left alternately, results in the production of a bostryx or a cincinnus respectively.

4. The transformation of the inflorescence from an aggre-

gate dichasium to a raceme through various modifications of the thyrse is traced amongst the species of the genus *Forsteronia*. This progression has evidently been actuated by the progressive reduction in acropetal fashion of both the decussate pairs of branches of an aggregate dichasium.

5. The spike is derived from the raceme; the corymb and the umbel are derivative from both determinate and indeterminate inflorescences.

6. Solitary flowers, whether terminal or lateral, are apparently derived from a previous condition of pluriflory through the agency of reduction.

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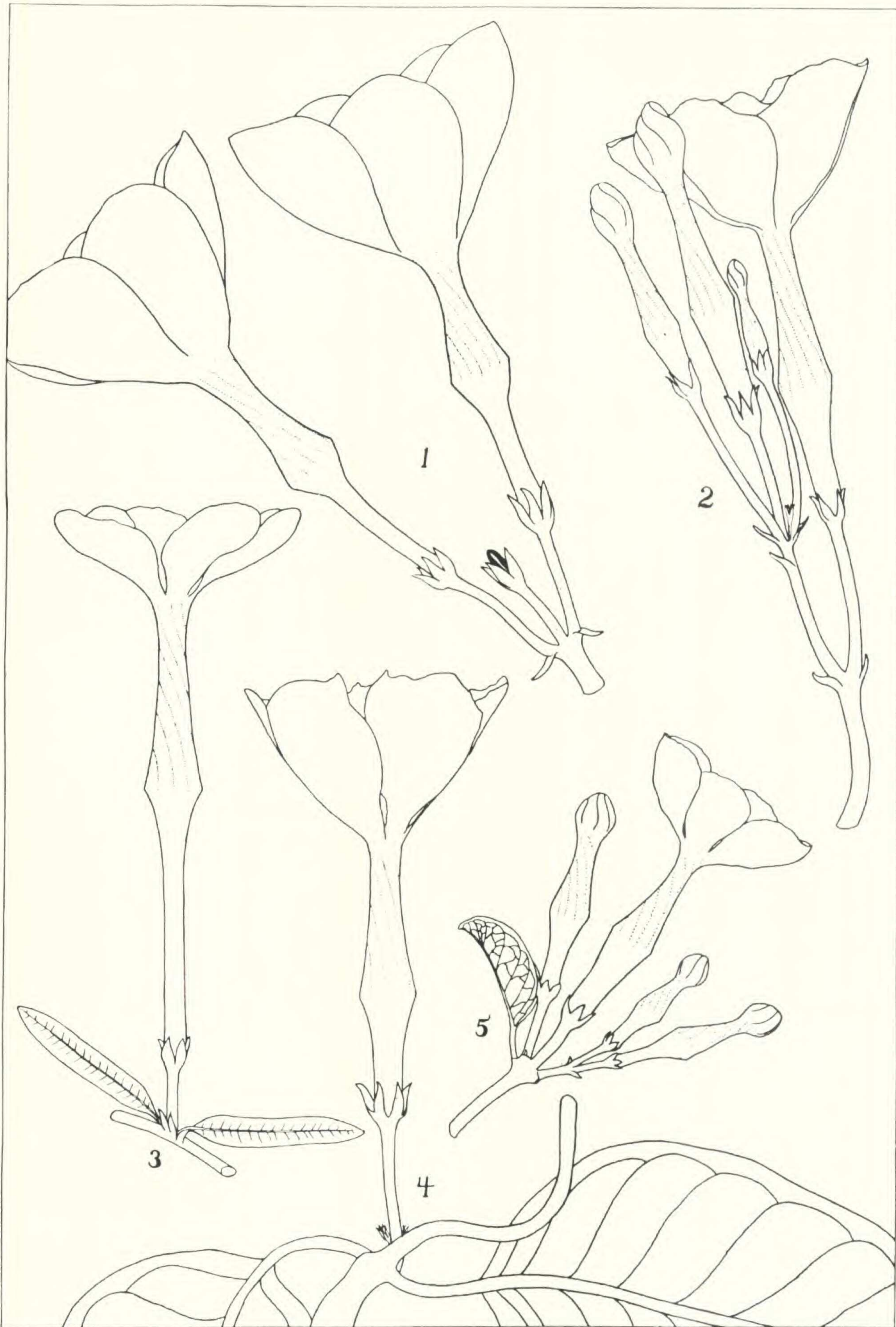
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EXPLANATION OF PLATE

PLATE 1

Figs. 1-2, 4-5. Variation in inflorescence structure amongst individuals of *Echites umbellata* Jacq.

Fig. 3. Inflorescence structure of *E. crassipes* A. Rich.

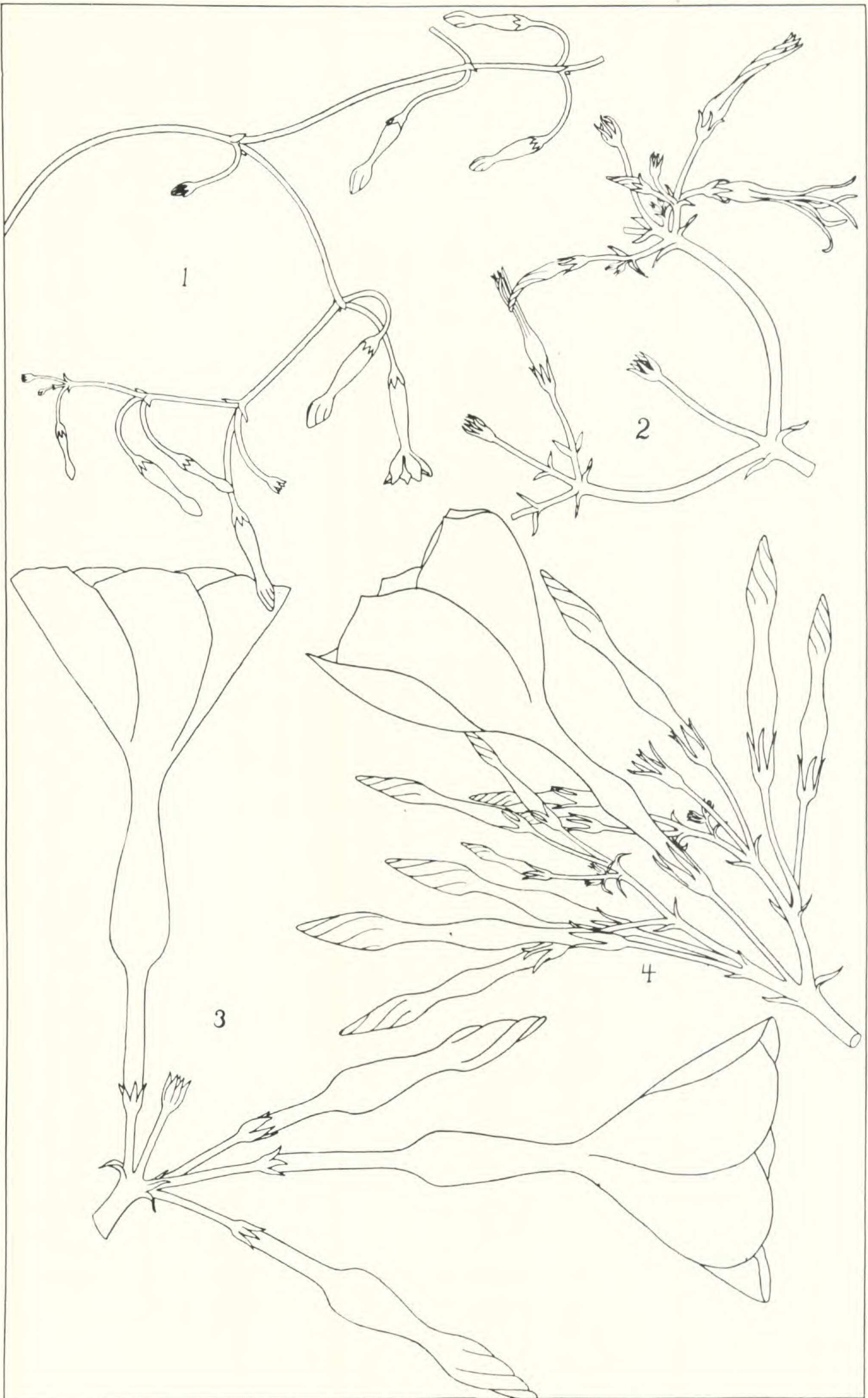


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## EXPLANATION OF PLATE

## PLATE 2

- Fig. 1. *Echites tuxtzensis* Standl.  
Fig. 2. *E. turbinata* Woods.  
Fig. 3. *E. yucatanensis* Millsp.  
Fig. 4. *E. turrigera* Woods.



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## EXPLANATION OF PLATE

## PLATE 3

- Fig. 1. *Prestonia agglutinata* (Jacq.) Woods.  
Fig. 2. *Malouetia Schomburgki* Muell.-Arg.  
Fig. 3. *Fernaldia pandurata* (A.DC.) Woods.  
Fig. 4. *Thenardia floribunda* HBK.  
Fig. 5. *Macrosiphonia longiflora* (Desf.) Muell.-Arg.



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